

# THOUGHTS ON THE ORIGIN OF INSECT FLIGHT<sup>1</sup>

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**ABSTRACT:** It is suggested that early Paleozoic landscapes were characterized by extensive seepage areas which provided relatively stable environmental conditions for early apterygotes. Increased dependence on the aquatic environment is envisioned as directing the development of pleural respiratory folds which could be ventilated by subcoxo-coxal muscles; pleural folds are not considered to be derived from preexisting insect structures such as paranota or coxal styli. It is also suggested that wing development may have been influenced by a thermoregulatory or swimming function of wings, or both. Flight is considered to have evolved in the reproductive adult stage in response to a continuous downstream displacement during the juvenile stage: flight eventually augmenting other forms of locomotion during the migration to upstream oviposition and nursery areas. The polyphyletic origin of wings is considered improbable, although the Protodonata and Odonata are considered to be the sister group of remaining Pterygota. Further, it is suggested that if the small stream theory is similar to the actual course of events then it is probable that pertinent fossil evidence will be scarce due to the high energy nature of the small stream environment.

Speculation concerning past evolutionary events is perhaps the most intriguing aspect of evolutionary study, although inherently the most problematic. Evolutionary scenarios are based on the determination of character state polarity as are cladograms and phylogenies, but the impetus for their conception lies beyond morphology, being primarily to achieve an understanding of the evolution of function. This is a noteworthy virtue as adaptive radiations are often triggered by functional adaptations of preexisting structures. A well-known example concerning preadaptation of flight involves the fossil "bird" *Archaeopteryx* which displays feathered wings and tail but lacks a well-developed breastbone for flight muscle attachment. The most ancient pterygote or winged insects are the Palaeoptera (a paraphyletic group with living representatives being the Ephemeroptera and Odonata) characterized by the inability to withdraw the wings into a folded arrangement flat over the abdomen. The abdominal gill plates of palaeopteran nymphs are obvious candidates for preadapted wings and have been suggested as such by several authors.

The origin of insect flight has been the subject of considerable speculation, the most favored scenario currently being the paranotal theory of Muller (1873-75). However, the paranotal theory did not receive general acceptance until Crampton (1916) considered, apparently incorrectly, insect wings to be of tergal origin. Crampton's version of the paranotal theory proposes that protective thoracic paranota first acted as parachutes,

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then as gliding and steering wings, and finally as flapping wings. The considerable discontinuity between gliding and flapping paranota is also an objectionable supposition of the theory and has led to the proposal of several alternative theories incorporating the idea of the preadapted "flapping" wing. The majority of these alternatives have involved an aquatic-related origin of insect wings: Woodworth (1906) proposed the origin of wings from gill opercula (gill-plates), Bradley (1942) and Grant (1945) from swimming gills, and Wigglesworth (1973, 1976) from gill plates derived from coxal styli. Rasnitsyn (1981) has proposed the origin of wings from movable structures which supposedly fused with the tergum and then again became movable coincident with the development of flight. In the present paper it is suggested that the environment of Paleozoic spring seeps provided suitable conditions for the evolution of insect flight, that wings originated from pleural respiratory folds ventilated by what are now the flight muscles, and that wing development may have been influenced by a swimming or thermoregulatory function, or both.

#### DISCUSSION

##### Mid-Paleozoic Terrestrial Environments

Silurian spring seeps may have been widespread, offering hospitable habitats to the early apterygote insects. Possible soil bacteria discovered in the Gowganda formation of Ontario suggest the presence of soils by the Mid-Prepaleozoic, and the textural and compositional maturity of Cambrian terrigenous sediments compared to those of the Ordovician suggest the development of soils and terrestrial plants by the Mid-Paleozoic (Dott and Batten 1971). Land plants appeared at least by the Silurian and by the late Devonian diverse lowland forests existed in eastern North America, Greenland, and Britain (cf. Andrews 1961). Fossil winged insects show considerable diversity in carboniferous rocks, indicating, as in the case of land plants, an earlier origin than documented by known fossils. Silurian terrestrial plants included the psilophytes (Dott and Batten 1971) and probably also lichens, liverworts, mosses, and primitive ferns. This low and shallow-rooted vegetation would reduce runoff and evaporation, and although evapotranspiration would occur it would be much less than that associated with later more deeply rooted plants (cf. Hibbert 1967). These conditions would favor the accumulation of vast ground water reserves and the widespread formation of seepage areas. Therefore, seepage areas and spring-fed streams may have characterized large portions of the Paleozoic landscape at a time coinciding with the origin of insect wings and flight.

Seepage areas, springs, and spring-fed streams would afford a somewhat discontinuous but stable environment to the early apterygotes. Emerging

groundwater generally remains at about the average annual air temperature, has stable chemical characteristics, and is relatively abundant in nutrients although oxygen concentrations near the source are typically lower than that of the atmosphere. Mid-Paleozoic seeps were probably only partially shaded by plants and therefore supported the growth of green algae which in addition to the inflow of allochthonous material formed the basis of innumerable productive seepage communities. It is clear that ancient apterygotes would be attracted to seepage areas, even though it is likely they originally inhabited the terrestrial environment.

### Life History and Morphology of Protopterygota

The life history of protopterygotans is likely best approximated among living forms by that of the Archaeognatha (Machilidae). A semiaquatic way of life for the Protopterygota is supported by the habitat requirements of archaeognathan genera such as *Allomachilis* and *Petrobius* which live in the damp crevices of coastal cliffs. Heeg (1967) found archaeognathans much more susceptible to dehydration than thysanurans, and Smith (1970) found that if mienertelids, the most primitive archaeognathans, were deprived of water in droplet form they would die in two or three days. In addition, the aquatic nymgal stage of extant Palaeoptera and primitive Neoptera (i.e. Plecoptera) also suggests that protopterygotes were semiaquatic. It is likely that the protopterygotes were characterized by an ametabolous development which included several instars after the attainment of sexual maturity, indirect sperm transfer which was accomplished in the terrestrial environment via the substrate, and exophytic oviposition probably in moist detrital material. The diet probably combined items consumed by archaeognathans and ephemeropterans such as algae, diatoms, lichens, microscopic organisms, and detritus, all of which are generally relatively abundant in or near spring seeps. Smith (1970) reported that the archaeognathan *Machilinus* is attracted to warm surfaces, which indicates that protopterygotes were likely attracted by the stenothermal environment of spring seeps.

Protopterygotan morphology was evidently characterized by a pronounced serial homology of body parts (Fig. 1), although the specialization of body segments had already led to the formation of insectan tagmata, as evidenced by the morphology of Archaeognatha and fossil Monura. The mandibular, maxillary, labial, thoracic, and abdominal segments bore paired coxae, with each coxite in turn apparently bearing a lateral telopodite (leg), a sensory stylus, and an absorptive organ or vesicle. Snodgrass (1954) considered apterygote abdominal styli to be homologous with the lateral abdominal gills of Ephemeroptera and Zygoptera; and Wigglesworth

(1973) considered archaeognathan coxal and abdominal styli, and ephemeropteran gill-plates homologous with wings. However, Smith, (1969, 1970) considered abdominal styli telopodites, and archaeognathan thoracic styli homologous with apterygote vesicles and gonapophyses. Smith's interpretation is supported by the presence of segmented abdominal styli in some fossil Palaeoptera (Kukalova-Peck 1978). Several workers have considered gill plates to be serially homologous with wings, and venational patterns of gill-plates noted by Woodworth (1906) have also been demonstrated in the abdominal "wings" of Palaeozoic nymphs (Kukalova-Peck 1978). Wings are always found above the spiracle and telopodites below the spiracle (Snodgrass 1935). Landa (1948) has shown the intermediate position of the spiracle between the dorsal gill-plate (wing) trachea and telopodite tracheae of ephemeropteran nymphs. The position of vestigial "abdominal wings" above the spiracles of certain adult Ephemeroptera (Birket-Smith 1971) and the position of leg-derived male forceps below the spiracles also support this arrangement. It is also noted that the lateral abdominal gills of certain zygopteran nymphs may be homologous with those of the Ephemeroptera as indicated by their position with respect to the developing female gonocoxae. According to Kukalova-Peck (1978), Durken (1907, 1923) reported that gill-plates arise from

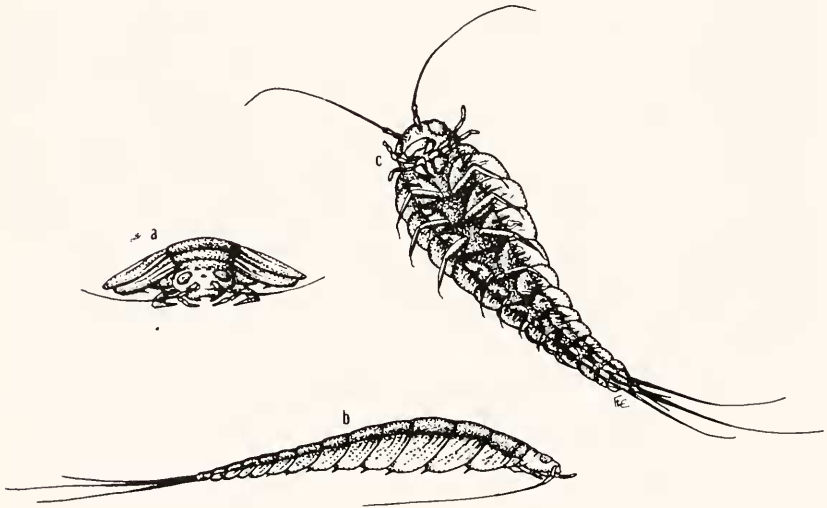


Figure 1. Hypothetical protopterygota: (a) anterior view of subadult, (b) lateral view of subadult, and (c) lateroventral view of adult in gliding posture; length of body 10-15 mm.

pleural evaginations above the spiracles which migrate with consecutively older instars toward the terga, as do the thoracic wings (Tower 1903; Bocharova-Messner 1959, 1965, 1968). However, Matsuda (1981) claims that Durken's work on *Ephemerella ignita* supports the tergal origin of ephemeropteran gills. Unfortunately, the gills of *Ephemerella* are highly specialized in their dorsal position, indicating that study of forms such as *Ameletus*, *Siphloplectron*, or *Isonychia* may clearly support a pleural origin of ephemeropteran gills. Dorsal migration of stylus-derived wings proposed by Wigglesworth (1973, 1976) would be blocked by the subcoxal annulus which E.L. Smith (Kuklova-Peck 1978) believes was developed in primitive apterygotes since it occurs in both recent Archaeognatha and fossil Monura. Paleozoic nymphs have been found with articulating "wings" on three thoracic and nine or ten abdominal segments (Carpenter 1935, Kukalova 1968). As shown by Kukalova-Peck (1978) the immobile nature of recent nymphal thoracic wings is secondary and does not support the origin of wings from paranota. Therefore, the apparent desirability of proposing the origin of wings from old structures such as paranota or coxal styli is vacuous, wings being likely derived from new structures arising from the pleural region above the spiracles.

### Origin of Preflight Wings

The possibility that wings are entirely new insect structures greatly increases the array of scenarios which may explain their origin. Bocharova-Messner (1971) suggested the origin of wings from spiracular flaps which served sensory and protective functions related to respiration. In addition, Kukalova-Peck (1978) suggested that spiracular flaps may have served as opercula to close spiracles while under water, or to prevent water loss while on land; and Woodworth (1906) considered wings to be derived from gill plates which were used to ventilate and protect filamentous gill-clusters. Indeed, the abundance of plesiomorphic character states attributable to aquatic juveniles indicate that terrestrial apterygotes invaded the aquatic environment and that the origin of wings was somehow related to a change in respiratory function. In addition, an original respiratory function of the wings is somewhat supported by the wing pad spreading behavior of various Zygoptera in response to low oxygen levels.

A transition to aquatic respiration would be favored by the unique environment of the seepage area. Protopterygotes attracted by an abundant food supply and stable temperatures would encounter high oxygen concentrations during daylight due to photosynthetic activity. Low oxygen levels may have occurred after nightfall due to both the low oxygen content of emerging ground water and a substantial biological oxygen demand. The lowest oxygen concentrations would then coincide with the time of maximum

possible benefit from the stenothermal nature of spring seeps. The wide range in oxygen concentrations possibly allowed a gradual increase in the efficiency of aquatic respiration. Plastrons (air cells) and the absorption of oxygen through the membranous pleural region were likely the initial mechanisms of aquatic respiration, and it is possible that setae present on the developing wing buds of recent insects may be vestiges originally used in the retention of plastrons. Increased dependence on the aquatic environment would select for a dendritic-like development of small tracheal branches above and lateral to the spiracles to aid in the distribution of oxygen through the original tracheal system. This could be augmented by the development of pleural folds on the thoracic, abdominal, and possibly the maxillary and labial segments to increase pleural surface area. Such folds apparently occur in the Archaeognatha. Pleural folds would be preadapted for ventilation by the subcoxo-coxal muscles which would distort a membranous pleural region during walking, and it is perhaps significant that tergal-sternal muscles could also aid in ventilation by compressing the pleural region. These muscles would represent the primitive direct and indirect flight muscles, respectively. It is likely that the uppermost gill folds would become operculate both for ventilation and protection of the more delicate inner gills. A review of the literature reveals that elements of this sequence were first proposed by Oken (1811), Lang (1888), and Woodworth (1906). Efficiency could be improved by increasing the surface area to volume ratio through a flattening and expansion of the protowings. However, maintenance of sufficient blood flow through the protowings would require internal modifications.

### Preflight Wing Venation

Kukalova-Peck (1978) suggested that the haemocoel was restricted to channels which later became cuticularized and sclerotized to form a stiffening venational framework. Fluting was supposedly achieved by a differential excretion of cuticular material on the veinal tubes, and blood circulation achieved by a refluxing of blood into and out of six basal vein openings. If convex veins were primitively formed on the dorsal wing surface and concave veins formed on the ventral surface, then an alternate scenario is suggested. It is noted that this condition apparently persists as a plesiomorphic character state in at least ephemeropteran wings (Spieth 1932), wing pads, fossil wing pads (Carpenter 1979), and possibly gill-plates; and in nymphal odonate wings (Calvert 1911), and wing pads. Nonalignment of blood channels and venation in the nymphal wings of recent insects is here considered an adaptation of the lacunae to subsequent changes in wing function. It is possible that as the protowings became flattened, a septum was formed between the dorsal and ventral surfaces to

maintain a sufficient blood flow (Fig. 2). Accessory dorsal pulsatile organs were eventually utilized, although gravity probably maintained the circulatory gradient in the earliest wings. The dorsal convex chasm was the efferent route and the ventral concave chasm afferent. In addition to the obvious functions of blood circulation in the wing such as the transfer of nutrients and hormones, the blood transfers heat which may have been its most important function in the wings of early insects.

### Preadaptation of Protowings

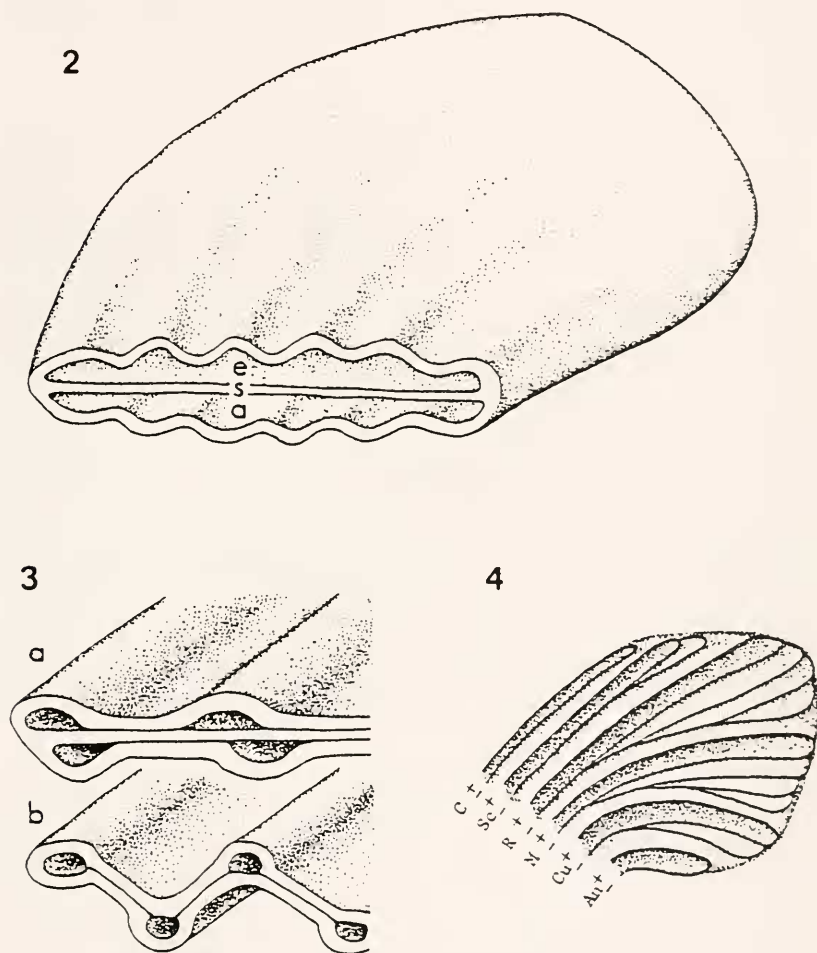
Prothoracic winglets of adult Palaeodictyoptera and wings of Paleozoic nymphs are characterized by a tubular cuticularized venation, a slight corrugation, and a hinge comprised of tergal sclerites and enlarged vein bases suggesting that preflight wings were significantly preadapted for flight (Kukalova-Peck 1978). The possibility of a preadapted hinge indicates that preflight wings were utilized in a flapping manner, either as gill opercula (Woodworth 1906) or possibly as spiracular flaps (Bocharova-Messner 1971). However, since corrugation and copious venation are not needed in the gill-plates of recent insects, it is possible that additional selective pressures acted in their development, notably the need to control body temperature. A semiaquatic insect adapted to the stable temperatures of emerging ground water would certainly benefit from a system which regulated body temperature while entering the terrestrial environment for reproductive purposes. Such a system is apparently utilized by the Odonata for either "heating up" in the morning or "cooling down" at midday; the system involves the wing, its circulatory system, and its variable orientation with respect to the sun. Certain fossil Palaeoptera have the dorsal veins hyperdeveloped suggesting a thermoregulatory function in early wings. The transition of gill opercula to structures useful in thermoregulation could occur in the humid microenvironment of the spring seep, and it is noted that the caudal gills of certain Zygoptera such as *Megalagrion* are surprisingly resistant to damage while the nymph scampers about in the terrestrial environment. A thermoregulatory function in early wings would be enhanced by the increase of wing size which would require an associated venational framework for support and heat transfer. In addition, corrugation would aid support, allow for a greater surface area, and provide for zones of shading and air pockets. It is evident that the dorsal and ventral blood chasms of the wing were reduced to five or six rib-like veins which contained tracheae and nerves as well as blood. Possibly, convex veins were originally located directly above concave veins so that the dorsal-ventral dimension of wing corrugation developed before the anterior-posterior dimension (Fig. 3). As the dorsal veins have apparently slipped forward, a suitable wing vein notation slightly modified from that of Kukalova-Peck (1978) would be:

costa anterior (CA+), costa posterior (CP-), subcosta anterior (ScA+) subcosta posterior (ScP-), radius anterior (RA+), radius posterior (RP-), media anterior (MA+), media posterior (MP-), cubitus anterior (CuA+), cubitus posterior (CuP-), anal anterior (A+), and anal posterior (AP-). However, evidence for recognizing CP- and Sc+ is weak because the anterior wing margin questionably represents a vein, and Sc+ is vestigial when apparent. Improvements of the hinge involving a thickening of wing vein bases and a thinning of the wing in general coupled with changes in venation to improve a thermoregulatory function of wings would lead to the modification of the original blood flow pattern. The concave (ventral) veins may have become multilooped in order to increase shading efficiency by increasing the width of troughs (Fig. 4). This process of looping was apparently carried to some dorsal veins, but vein pairs in the anterior wing region were probably not involved at all in order to maintain strength along the leading edge of the wing. Major vein pairs became fused basally and cross veins allowed the eventual anterior-posterior blood flow of existing Pterygota.

A thermoregulatory function of the wings not only offers a possible explanation for the increase in wing size and the development of venation and corrugation in the preflight wing, but may explain the muscular and articular changes necessary for pronation and supination. It is apparent that early insects could regulate their temperature while in the terrestrial environment by varying body orientation with respect to the sun, but considering only the wings it is obvious that at low angles of inclination only slight reorientations of the wings are necessary to regulate body temperature. This effect is particularly enhanced when the corrugations are characterized by wide troughs and oriented perpendicular to incoming light. Therefore, rotation and the associated modifications of the wing base can be considered an adaptation to thermoregulation and a preadaptation to flight.

Bradley (1942) and Grant (1945) have suggested that preflight wings became adapted for flight by serving as fins and propulsion devices in water. However, the original use of gill plates in swimming would probably not be similar to the gill-plate method employed by nymphal mayflies such as *Chloeon*, or the method used by certain adult Chalcid wasps which swim under water with their wings. The original hinge was apparently straight, wide, and parallel to the body axis. Swimming, if achieved, was likely accomplished by undulating the body in an up and down fashion while altering the pitch of the gill-plates. The gill-plates could be tilted with the subcoxal-coxal muscles (precursors of the direct flight muscles), which is a possible explanation for the muscular and articular changes necessary for pronation and supination. However, the development of pronation and





Figures 2-4. Hypothetical insectan protowings illustrating a possible scenario leading to the formation of corrugation and venation.

Figure 2. Section through protowing distal to hinge, note formation of septum: (s) septum, (a) afferent chasm, (e) efferent chasm.

Figure 3. Formation of corrugation and venation: (a) primary dorsal-ventral corrugation, (b) secondary anterior-posterior corrugation.

Figure 4. Branching or looping of the posterior (ventral) veins.

supination of gill-plates to improve the ventilation of inner gills may have been a preadaptation for both swimming and flying.

### Development of Flight

The development of flight, like the origin of wings, was quite possibly brought about by conditions in the small stream environment. Life history was likely segregated into a semiaquatic juvenile stage and a terrestrial adult stage. However, it is noted that Kukalova-Peck (1978) believes that metamorphosis did not evolve until much later and occurred several times in the Pterygota. The nymphal stage would be primarily a period of feeding characterized by a substantial increase in body size; in contrast the adult stage would be primarily concerned with reproduction. A continuous downstream displacement, or drift (cf. Waters 1972), characterized the nymphal stage which was compensated for by an upstream migration during the adult stage. Wigglesworth (1963, 1973, 1976) proposed that semiaquatic pterygotes "learned to fly" after being swept up by the thermal upcurrents of semiarid regions to be deposited with the next rainfall. However, advantages accrued to adults while migrating to upstream reproductive areas also seem a plausible explanation for the origin of flight. Upstream migration was probably achieved through a combination of walking, swimming, jumping, and eventually gliding and flapping flight. The author has observed primitive archaeognathans jumping from the surface of water, and primitive ephemeropterans (*Isonychia*) jumping back into water when disturbed while out of water to emerge. The author has also observed *Isonychia* to "swim" out of water into the air when startled; it is perhaps significant that this ability is developed in forms inhabiting rapid streams. Although these primitive forms do exercise some attitude control in flight, presumably with the cerci, legs, and antennae, Flower (1964) has calculated that attitude control and gliding distance would be improved in small insects with even rudimentary wings. This suggests that even small articulating lateral gill opercula might be advantageous in flight. Evening updrafts through stream valleys could have helped carry the early pterygotes to the upstream mating and nursery areas, and downstream drift of nymphs to areas containing unexploited food resources would gradually lengthen migratory routes and necessitate the gradual improvement of gliding and flapping flight. The specialization of the ovipositor for laying eggs in the protective environment of living and dead plant material surrounding seepage areas could lead to a further consolidation of reproductive sites and also to intense sexual selection between males which would probably involve flight capabilities. Increased vagility coupled with the isolated nature of reproductive areas would then set the stage for a dramatic adaptive radiation.

## Monophyletic Origin of Wings

Matsuda (1981) has revived the polyphyletic origin of insect wings originally proposed by Lemche (1940). Matsuda suggests the origin of the Eupalaeoptera (Protodonata and Odonata) from the Archaeognatha, and the origin of the Neopalaeoptera (Protephemrida, Ephemeroptera, Palaeodictyoptera, and Megasecoptera) and Neoptera (remaining Pterygota), from the Thysanura. Although an original dichotomy between the Eupalaeoptera and remaining Pterygota seems well-founded, a polyphyletic origin of wings seems doubtful. Matsuda's conclusion was reached by considering certain similarities of the Archaeognatha and Odonata synapomorphic (derived characteristics held in common), when they are as reasonably considered symplesiomorphic (primitive characteristics held in common) or a result of convergence. Primary justification for the character state polarities determined by Matsuda is his belief that the considerable autapomorphy (unique derived characteristics) of the Eupalaeoptera cannot be explained by ecological divergence. However, all eupalaeopteran autapomorphy may be explained by what appears to be a basic ecologic dichotomy of the Pterygota, that is between "predator and nonpredator", a dichotomy which is repeated within later orders such as the Plecoptera and Coleoptera. Of the several eupalaeopteran autapomorphic thoracic characteristics listed by Matsuda (1981), all can be explained by the need to increase flight agility. Furthermore, the unique wing venation of the Eupalaeoptera (supposed absence of MP and CuA) can be explained by the basal fusion of longitudinal veins (Carle 1982a), again in response to the need for increased flight agility and not due to a unique origin of eupalaeopteran wings.

Matsuda considered the large compound eyes "which almost meet dorsally in Anisoptera and Machilidae" symplesiomorphic. However, annectants reveal this similarity to have developed through convergence. Symplesiomorphic characteristics of the Archaeognatha and Eupalaeoptera probably include: presence of four intratergal apophyses, presence of the pseudoprescutum, absence of the indirect flight mechanism, and the absence of contact between the primary genitalia during sperm transfer. The latter characteristic is again likely related to the predatory nature of the Eupalaeoptera (Carle 1982b). It is probable that ancient eupalaeopteran males used the cerci to guide females to their spermatophores (as in at least some archaeognathans), and eventually developed the tandem hold to prevent being eaten by the female. The eupalaeopteran copulatory process then developed with its unique secondary copulatory apparatus, sperm removal, and male above copulatory position. In contrast, in the Ephemeroptera and Neoptera the primitive copulatory position of the female is above the

male, and the presence of ephemeropteran-like forceps on the ninth sternum of male Palaeodictyoptera (Kukalova 1970) supports the female above copulatory position in all noneupalaeopteran Pterygota. Other synapomorphic character states of the Neopalaeoptera and Neoptera are related to the development of the indirect flight mechanism in which the downstroke is achieved by contraction of longitudinal dorsal muscles which restore curvature to momentarily flattened pterothoracic terga, these include: partial fusion of the thoracic terga and pleura, specialization of several muscles (cf. Matsuda 1981), differentiation of the nodal wing processes, and apparent differentiation of the proximal portion of the axillary plate into the second and third axillary sclerites. The Neoptera are further specialized in the integration of the third axillary sclerite into a unique wing folding mechanism. Similarities of the Thysanura and noneupalaeopteran Pterygota which have been suggested as synapomorphic by Matsuda (1981) may of course be due to convergence. It is also possible that the Thysanura represent an early Neopalaeopteran group which became secondarily wingless.

### Fossil Protopterygota

The small stream theory concerning the origin of insect wings and flight has many implications if it does indeed depict the true course of events. Foremost are implications concerning the abundance and distribution of early pterygote fossils. If the assumption concerning the thermoregulatory function of preflight wings is correct; then regions of the Devonian geography characterized by seasonal climates may yield enlightening fossil evidence; these areas include Siberia, Greenland, and the southern continents as evidenced by the occurrence of Paleozoic "tree" rings (cf. Dott and Batten 1971). The high energy environment of the small stream is certainly not a suitable environment for insect fossilization, leaving a bias in the fossil record toward relatively advanced forms which lived near swamps and lakes. However, Rasnitsyn (1981) states that the "chances of fossilization were much higher for aquatic and amphibious insects than for terrestrial ones." Rasnitsyn's belief seems doubtful in light of the author's experience in carefully processing benthic lake and stream samples (cf. Carle 1980). Insect remains were primarily of hard-bodied terrestrials, typically Coleoptera. This is apparently related to both the higher population levels and higher durability of terrestrial insects. Therefore, bias in the insect fossil record is probably toward a disproportionate representation of coleopteroids and orthopteroids. However, the importance of fossil evidence in determining the correct phylogenetic classification of insects must not be underrated in light of the considerable degree of parallel evolution likely after the origin of insect flight.

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## BOOKS RECEIVED AND BRIEFLY NOTED

A BIOSYSTEMATIC STUDY OF THE EUROPEAN STRATIOMYIDAE (DIPTERA). VOL. 1. Rudolf Rozkosny. 1982. Dr. W. Junk, Pub. 401 pp. \$79.50.

A biosystematic revision of the European Stratiomyidae, summarizing basic information on morphology, biology, ecology, distribution, economics, and taxonomy. Vol. 1 contains introductory sections and the systematics of the Beridinae, Sarginae and Stratiomyinae subfamilies.